

Global coal gap between Permian–Triassic extinction and Middle Triassic recovery of peat-forming plants

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ABSTRACT

Early Triassic coals are unknown, and Middle Triassic coals are rare and thin. The Early Triassic coal gap began with extinction of peat-forming plants at the end of the Permian (ca. 250 Ma), with no coal known anywhere until Middle Triassic (243 Ma). Permian levels of plant diversity and peat thickness were not recovered until Late Triassic (230 Ma). Tectonic and climatic explanations for the coal gap fail because deposits of fluctuating sea levels and sedimentary facies and paleosols commonly found in coal-bearing sequences are present also in Early Triassic rocks. Nor do we favor explanations involving evolutionary advances in the effectiveness of fungal decomposers, insects or tetrapod herbivores, which became cosmopolitan and much reduced in diversity across the Permian–Triassic boundary. Instead, we favor explanations involving extinction of peat-forming plants at the Permian–Triassic boundary, followed by a hiatus of some 10 m.y. until newly evolved peat-forming plants developed tolerance to the acidic dysaerobic conditions of wetlands. This view is compatible not only with the paleobotanical record of extinction of swamp plants, but also with indications of a terminal Permian productivity crash from $\delta^{13}\text{C}_{\text{org}}$ and total organic carbon of both nonmarine and shallow marine shales.

INTRODUCTION

It is a curious fact that no coal seam of Early Triassic age has yet been discovered, and those of Middle Triassic age are rare and thin. In this paper we demonstrate this striking lacuna in coal formation. We also attempt to understand why there is such a gap, using evidence from stratigraphy, coal geology, paleosols, and fossil fungi, plants, and animals.

A number of possible explanations for the coal gap have been advanced. Land masses of the world may have been riding too high with respect to sea level for the accumulation of peat (Daragan-Sushchov, 1989; Faure et al., 1995). Naturally acidic swamps may have been overwhelmed by additional acid, such as sulfuric acid from SO_2 of massive eruptions of the Siberian Traps (McCartney et al., 1990), or nitric acid from NO_x generated by impact of a large extraterrestrial bolide at the Permian–Triassic boundary (Zahnle, 1990). Global climate may have changed from an icehouse with wet and cool climatic zones to a greenhouse that was too hot and dry for peat (Worsley et al., 1994). Microbes such as fungi may have become more effective or herbivory by insects and tetrapods more destructive in Early Triassic wetlands (Moore and Worsley, 1994). Finally, plants may have re-evolved adaptations to peat swamps well after the end-Permian extinctions (Ziegler et al., 1993). Some of these possible explanations invoke events at the Permian–Triassic boundary, others postulate long-term hostile conditions. A variety of paleontological and geological lines of evidence are considered here on both short and long time scales.

A marine parallel to the coal gap is Flügel's (1994) Early Triassic "reef gap." Common features of tropical reefs and peat swamps provide additional clues to the reasons for their Early Triassic disappearance.

EVIDENCE FROM STRATIGRAPHY

The oldest known permineralized peats and cuticle coals are Early Devonian (Kidston and Lang, 1921; Krassilov, 1981), and the oldest woody coal is Late Devonian in age (Gillespie et al., 1981). Ever since then, there has been a fossil record of peat-forming wetland ecosystems somewhere in the world. Early Triassic rocks, however, lack

coal or permineralized peat. Veevers et al. (1994a) introduced the term "coal gap" for a sharp break between thick and widespread coal up to the Permian–Triassic boundary, lack of coal in the Early Triassic, followed by thin and uncommon coals in the Middle Triassic and thick and widespread coals in the Late Triassic (Fig. 1). The coal gap thus includes an absolute gap in the Early Triassic (Scythian) and recovery extending over the Middle Triassic (Anisian and Ladinian).

The rock closest to coal within the Early Triassic coal gap is 10 cm of carbonaceous claystone bearing the lycopsid plant *Pleuromeia* in the Newport Formation of southeastern Australia (Retallack, 1975). Reports of coal in Early Triassic rocks of northern Tibet (Deng et al., 1980; cited by Ziegler et al., 1993) are not reliable, because they are based on arbitrary placement of the Permian–Triassic boundary. There is no coal within the stratigraphic sequence between localities for Early Triassic ammonites and clams (Wen et al., 1981), but the Late Permian and Late Triassic of northern Tibet include coal (Li and Wu, 1981). We know of no Early Triassic coal anywhere in the world.

Middle Triassic coals are uncommon and thin (recovery of Fig. 1), like coals of the Devonian (Ergolskaya, 1936; Chi and Hills, 1976). Middle Triassic coals include the Cloughers Creek and Nymboida Coal Measures of New South Wales (Retallack et al., 1977, 1993), the Tank Gully and Long Gully Coal Measures of New Zealand (Retallack, 1979; Retallack and Ryburn, 1982), and the Lettenkohle of western Europe (Mader, 1990; Aigner and Bachmann, 1992). A breccia of permineralized peat blocks in the upper part of the Fremouw Formation of the central Transantarctic Mountains is also of Middle Triassic (probably Ladinian) age (E. L. Taylor et al., 1989; Farabee et al., 1989).

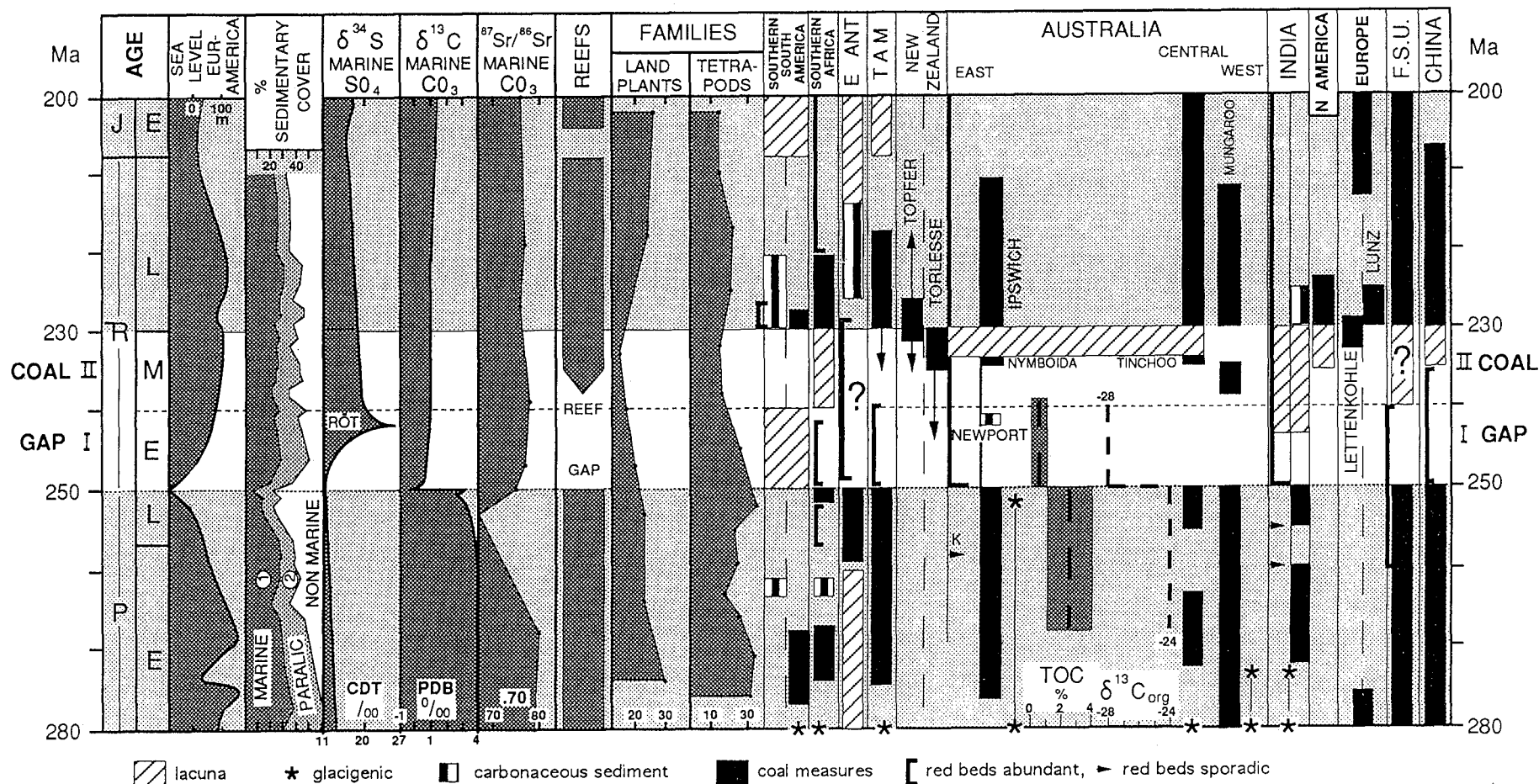


Figure 1. Distribution of Permian and Triassic coal and carbonaceous sediment on the Permian and Triassic Pangean platform and in the Chinese blocks related to global events. Time scale is from Palmer (1983), modified by the Permian-Triassic boundary calibrated at ca. 250 Ma (as in Veevers et al., 1994a). Sea level is measured against Euramerican platform; Permian (280–250 Ma) from Ross and Ross (1988, their Figs. 2–4), Triassic–Jurassic from Haq et al. (1988, their Figs. 16 and 17). Percent sedimentary cover of platform in marine, paralic, and nonmarine facies from Holser and Magaritz (1987, their Fig. 5); $\delta^{34}\text{S}$ in marine sulfate and $\delta^{13}\text{C}$ in marine carbonate from Holser et al. (1988); $^{87}\text{Sr}/^{86}\text{Sr}$ in marine carbonate from Koepnick et al. (1990) and Denison et al. (1994). Reef development from Flügel (1994), including a Scythian–earliest Anisian (250–238 Ma) “reef gap” followed by very rare later Anisian reefs and common Ladinian–Rhaetian reefs. An additional, tentative reef gap spanned the earliest Jurassic. Diversity (number of families) of land plants from Knoll (1984) and of tetrapods from Benton (1987). Glacigenic sediment, coal measures, carbonaceous sediment, and red beds along the Panthalassan margin of Gondwanaland—southern South America, southern Africa, Transantarctic Mountains (TAM), New Zealand, and eastern Australia into central and western Australia—are from Veevers et al. (1994b, their Fig. 3), with East Antarctic data from Webb and Fielding (1993) and Foster et al. (1994). Australian $\delta^{13}\text{C}_{\text{org}}$ and total organic carbon (TOC) from Morante et al. (1994) and Morante (unpubl. data); K = Kiama Sandstone. Indian data are from Veevers and Tewari (1995); data from North America, Europe, and China are from Veevers et al. (1994a); additional European occurrences from Aigner and Bachmann (1992) and Janoschek and Matura (1980); data from the former Soviet Union (F.S.U.) are from Nalivkin (1973).

The coal gap and recovery are emphasized by thick and productive coal measures of latest Permian age in the Sydney Basin of Australia (Diessel, 1992; Morante et al., 1994) and in the Kuznetsk Basin of Siberia (Gorelova et al., 1973; Betekkhina et al., 1984) on one side of the gap, and on the other, the Late Triassic (Carnian) Ipswich Coal Measures of Queensland (Mengel and Carr, 1976) and Productive Coal Measures Member of the Tuckahoe Formation of the eastern United States (Cornet and Olsen, 1990).

The beginning of the coal gap has been dated in eastern Australia as ca. 250 Ma by radiometric dating of biotite in tuff at the top of the coal measures (Veevers et al., 1994a). This is also the age of the Permian-Triassic boundary (250.0 ± 0.3 Ma) determined radiometrically in Chinese sections of high stratigraphic resolution (Claoué-Long et al., 1991; Renne et al., 1995).

The demise of peat formation also can be dated by chemostratigraphy using carbon isotopes of carbonate ($\delta^{13}\text{C}_{\text{carb}}$) and kerogen ($\delta^{13}\text{C}_{\text{org}}$). The Permian-Triassic boundary in marine sections in Eurasia, particularly along the margins of the former Tethys Ocean, is characterized by a sharp drop in $\delta^{13}\text{C}_{\text{carb}}$ of 3 per mil (Fig. 1; from +3 to 0 per mil; Holser and Magaritz, 1987; Baud et al., 1989) and a similar drop in $\delta^{13}\text{C}_{\text{org}}$ of ~3 per mil (from mean values of -24.6 to -27.4 per mil) in shale and marl interbedded with carbonate in Austria (Magaritz et al., 1992). Along the former margin of the Panthalassan Ocean in Canada, in deep-water marine sediment, the drop in $\delta^{13}\text{C}_{\text{org}}$ across the Permian-Triassic boundary is again ~3 per mil (from -29 to -32.6 per mil; Wang et al., 1994). The drop in $\delta^{13}\text{C}_{\text{org}}$ also can be traced from marine (Tethyan) sections in northwestern Australia to alluvial-paralic (Panthalassan) sections in southeastern Australia (Morante, 1993; Morante et al., 1994), and into the wholly nonmarine section of the Cooper Basin in the Australian continental interior (Morante, unpubl. data). There is also a precipitous drop in $\delta^{13}\text{C}_{\text{org}}$ at the Permian-Triassic boundary in eastern Australia between Permian coal measures below and coal-barren Narrabeen and Rewan Groups of the Sydney and Bowen Basins, respectively (Morante et al., 1994), thus revising the previous view from palynology that the Permian-Triassic boundary lay some hundred meters above the last coal below the base of the Narrabeen Group and correlative strata. Thus the coal gap began at the Permian-Triassic boundary.

Plant extinction as an explanation for the coal gap was supported by Morante et al. (1994), who showed that the boundary between coaly and coal-barren facies in eastern Australia coincided with the great extinction at the end of eastern Australian palynological zone 5 associated with the *Glossopteris* megaflores and the succeeding *Protohaploxylinus microcropus* palynozone representing the *Dicroidium* megaflores. In addition, the abrupt lightening of carbon isotopes in kerogen and carbonate carbon across the Permian-Triassic boundary may be due to lower levels of primary production along with oxidation of large amounts of buried carbon including methane clathrates, releasing carbon dioxide into the atmosphere as a greenhouse gas (Holser and Magaritz, 1987; Baud et al., 1989; Hsü and McKenzie, 1990; Erwin, 1993; Wang et al., 1994). This hypothesis is supported by the synchronous drop in $\delta^{13}\text{C}_{\text{org}}$ and total organic carbon in shale, from 1%–4% by weight in the latest Permian to 0%–1% in the earliest Triassic of Australia (Fig. 1).

Other environmental events also coincide with the onset of the coal gap. The drop in $\delta^{13}\text{C}_{\text{org}}$ in Australian sections, both marine and nonmarine, is ~4 per mil (Fig. 1; -28 to -24 per mil). The atmosphere is the only common reservoir for such widely scattered records of isotopic shifts on land and sea (Fig. 2), thus the shift probably coincided with a rise in atmospheric levels of CO_2 and global warming (Morante et al., 1994). Such global warming inferred from carbon isotopic data has been difficult to substantiate by other stratigraphic lines of evidence. It may be indicated by the wider paleolatitudinal spread of evaporite deposits in Triassic compared with Permian rocks; however, the role of warming in promoting the coal gap is weakened by similar evidence for continued global warming and drying into Jurassic time (Parrish et al., 1986).

Other sharp isotopic events, such as the Late (but not latest) Permian minimum value of $^{87}\text{Sr}/^{86}\text{Sr}$ in shallow marine carbonate (Denison et al., 1994), and the Early (but not earliest) Triassic $\delta^{34}\text{S}_{\text{sulfate}}$ peak, the Röt Event (Holser, 1984), occurred some millions of years before and after the Permian-Triassic extinction (Fig. 1). They were not so directly involved with the extinctions as the synchronous $\delta^{13}\text{C}_{\text{org}}$ shift. Strontium isotopic data give no support for theories of environmental acidification due to volcanism or bolide impact comparable to those proposed for the Cretaceous-Tertiary boundary (MacDougall, 1988). Nor does the

sulfur isotopic record show anything unusual at the onset of the coal gap, although the late Early Triassic sulfate sulfur isotopic spike may reflect a threshold in oceanic sulfate reduction resulting from rising levels of organic matter from increasing oceanic productivity (Holser and Magaritz, 1987) at a time of recovery from the coal gap.

The onset of the coal gap at the Permian-Triassic boundary was a time of exceptionally low sea level (Fig. 1) as determined by both sequence stratigraphy and the percentage of marine sedimentary cover (Holser and Magaritz, 1987; Ross and Ross, 1988; Haq et al., 1988). The curves show (1) low sea level for much of the latest Permian, when thick peats accumulated in Siberia, Australia, India and South Africa, and (2) marked transgression during the Early Triassic without evidence of peats. The coal gap and relative sea level are thus not related in a simple manner. Nor would one expect them to be, considering the many thick coal measures that have accumulated in intermontane basins remote from the sea (Mengel and Carr, 1976; Casshyap and Tewari, 1984; Betekkhina et al., 1984; Olsen, 1989; Taylor et al., 1990; Stricker, 1991; Wu et al., 1992). The exceptionally low sea level at the Permian-Triassic boundary has been explained by assembly of Pangea (Faure et al., 1995), but most of the supercontinent was already in place by ca. 320 Ma (Veevers, 1989), well before the onset of the coal gap at ca. 250 Ma. The resumption of thick coal measure accumulation at ca. 230 Ma coincided with rifting during an early phase in the breakup of Pangea (Fig. 2B; Veevers, 1989, 1990a).

Recovery from the coal gap can be dated in Australia and New Zealand, where thin coals reappear in the early part of the Middle Triassic (Anisian) near the first appearance of the biostratigraphically important seed fern *Dicroidium odontopteroides* and the halobiid bivalve *Aparimella apteryx* (formerly *Daonella*; Retallack et al., 1977; Retallack, 1979; Retallack and Ryburn, 1982; Campbell, 1994). These taxa appear in New Zealand before 242.8 ± 0.6 Ma (Retallack et al., 1993). Thick and productive coal measures of Late Triassic (Carnian) age in Queensland appear with the biostratigraphically important gymnosperm *Yabeia* (Retallack, 1977b), an event that is less well dated, but probably ca. 230 ± 5 Ma (Retallack, 1977b; Veevers, 1989). Similarly thin coals appear in the Middle Triassic (Ladinian) Lettenkohle of Europe (Mader, 1990; Aigner and Bachmann, 1992) and thick

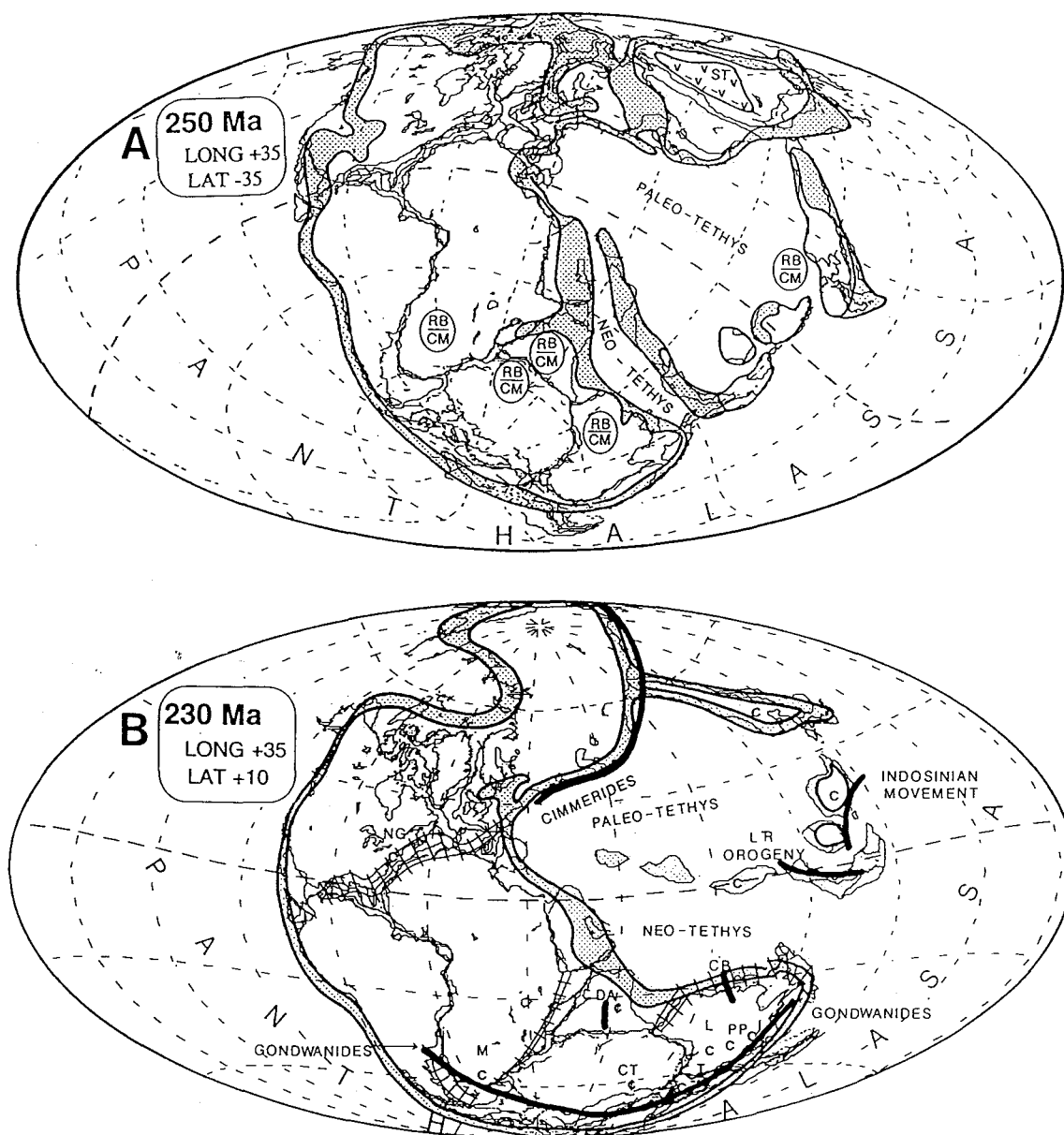


Figure 2. Pangea before and after the coal gap. Base map and paleolatitude drawn by computer from the Terra Mobilis program (Scotese and Denham, 1988). The center of the projection (Lambert equal-area) is given beneath the age and was chosen to concentrate the continents in the middle of the diagram. (A) At the Permian-Triassic boundary (250 Ma), modified from Veevers et al. (1994a). Places with the change from Permian coal measures to Triassic red beds are marked RB/CM. The shallow sea is shown by light stipple. Paleogeography is from Ziegler et al. (1979, their Figs. 38–43, for Kazanian), with addition of the Siberian traps (ST) marked by v's. (B) In the Carnian (230 Ma) or Late Triassic, modified from Veevers (1994). Deposition of coal (C) resumed in newly created rift basins in the eastern United States (Newark Group or NG; Olsen, 1989) and Australia (Ipswich Coal Measures or I, Peera Peera Formation or PP, Leigh Creek Coal Measures or L, and coal measures of Tasmania or T; Veevers, 1990b). Coal measures of the Molteno Formation (M) of South Africa (Dingle et al., 1983) followed the terminal (Gondwanide) deformation of the Cape Fold Belt. Carbonaceous sediment was deposited conformably on Early and Middle Triassic noncarbonaceous sediment in the central Transantarctic Mountains (CT; Collinson et al., 1994), ?Early–Middle Triassic red beds of the Jetty Member of the Flagstone Bench Formation in the Amery area of East Antarctica (Webb and Fielding, 1993; Foster et al., 1994), and in the Damodar River area of India (DA). In the Chinese cratons and Tibet, coal succeeds red beds (Yang et al., 1986). The coal and carbonaceous sediment were deposited during the start of continental rifting that prefigured rift oceans of the Atlantic and Indian Oceans (Veevers, 1989), and immediately after widespread deformation of the Gondwanides, Cimmerides, Indosinian Movement, and Malayan orogeny, and less intense folding and faulting in the Damodar River area (DA) of India and the Canning Basin (CB) of northwest Australia. Paleogeography is from Ziegler et al. (1983, their Fig. 2, Early Jurassic), but the (Late Triassic) Keuper of Europe is from Ziegler (1988, his Plate 10).

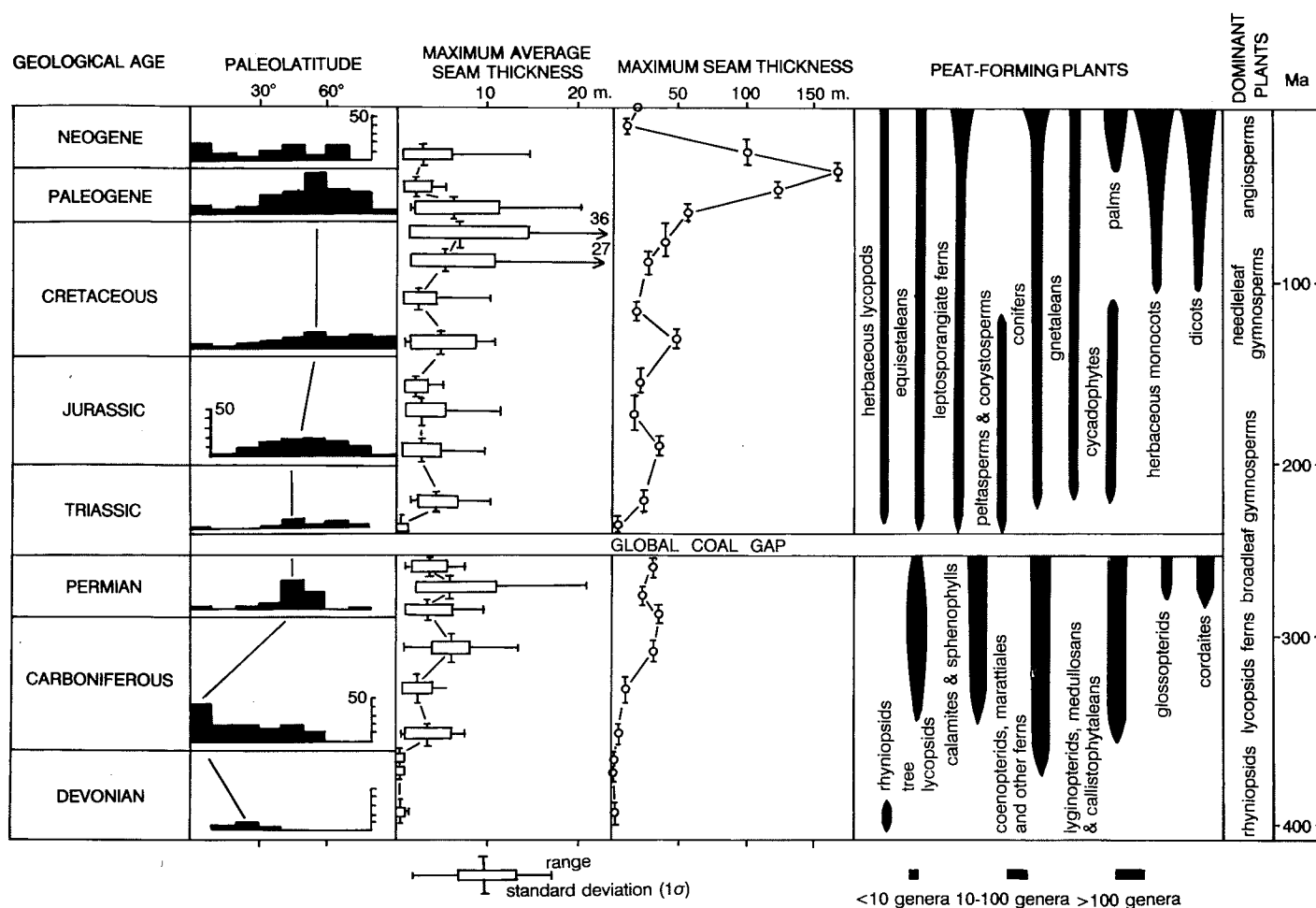


Figure 3. Long-term changes in coal paleolatitude, seam thickness, and coal-producing floras. Coal thicknesses include maximum values of unusually thick seams (to right) and (to left) averages of at least 10 coals within a single stratigraphic sequence (or 3 consecutive coals for Early Carboniferous and Devonian only). Paleolatitudes of coal occurrences were compiled from Habicht (1979). Coal thickness and floristic data are summarized in Tables 1–3, with floristic data supplemented by paleoecological studies of compression fossils in coal measures (Gorelova et al., 1973; Krassilov, 1981; Gillespie et al., 1981; Retallack and Dilcher, 1981; Meyen, 1982; Scheckler, 1986; DiMichele et al., 1987; Cornet and Olsen, 1990; Schneider, 1990; DiMichele and Phillips, 1994; Blackburn and Sluiter, 1994; Retallack, 1994).

coals in the Late Triassic (Carnian) Productive Coal Measures Member of the Tuckahoe Formation of Virginia, in the United States (Olsen and Cornet, 1990). Thus peat and coal formation ceased entirely for some 10 m.y., and coal seams as thick as those of the Late Permian were attained only after an additional 10 m.y.

EVIDENCE FROM COAL GEOLOGY

The coal gap interrupted long-term changes in the paleolatitudinal distribution of coals, in the thickness of coal seams, and in their petrographic composition, which could give clues to possible biological causes such as the coevolution of plants and fungi.

The earliest coals of Devonian age were mainly tropical and subtropical (Fig. 3). This remained the case during Carboniferous time when coal formed also at high latitudes. By Permian time most coals formed in temperate climatic belts of high latitudes, and this situation persisted into Triassic and Jurassic times. It was not until Tertiary time that coals once again became widespread in the tropics (Habicht, 1979). The marked paleolatitudinal shift of coals from tropical to temperate latitudes in the Late Carboniferous has been attributed to the evolution of tropical decomposers such as fungi and bacteria (Briden and Irving, 1964). Such an interpretation is debatable considering the abundance of fossil fungi in Carboniferous

coal balls (Stubblefield and Taylor, 1978), but there is no comparable indication of changing effectiveness of decomposers before or after the Early Triassic, and this falsifies the idea that decomposers are responsible for the coal gap (Moore and Worsley, 1994).

Further information on peat-forming ecosystems may be gained from the average thickness, range of thickness, and maximum thickness of coal seams through time (Fig. 3). Our compilation of maximum average thickness was culled from 141 published sequences with at least 10 consecutive seams, although this criterion was relaxed to only 3 consecutive seams for rare Early Carboniferous and Devonian coals (Table 1).

TABLE 1. MAXIMUM AVERAGE THICKNESS OF COAL SEAMS THROUGH TIME

Age	Mean (m)	Lowest (m)	Highest (m)	Standard deviation (m)	Seams (no.)	Locality	References
Miocene	3.47	0.06	15.40	3.31	27	Nenana, Alaska	Stricker (1991)
Oligocene	0.82	0.20	2.40	0.55	15	Golondrinas, Colombia	Suescún-Gomez (1978)
Eocene	2.00	0.40	5.20	1.77	11	Arauco, Chile	Flores-Williams (1978)
Paleocene	6.63	1.83	20.12	4.67	27	eastern Montana, U.S.A.	Matson and Blumer (1973)
Maastrichtian	6.97	0.61	36.58	9.28	14	Kaitangata, New Zealand	Harrington (1958)
Coniacian-Santonian	5.04	1.22	26.82	6.44	15	Adaville, Wyoming, U.S.A.	Glass (1981)
Aptian-Albian	2.46	0.60	10.40	2.97	10	Canmore, Alberta, Canada	McLean (1982)
Barremian	5.08	1.00	11.00	3.61	13	Eagle Mountain, British Columbia, Canada	Bustin and Dunlop (1992)
Callovia	2.08	0.74	4.24	1.13	10	Karaganda, Kazakhstan	Kushev (1963)
Bajocian	2.95	0.80	11.15	2.70	20	central Tadjikistan	Luchnikov (1982)
Toarcian	1.45	0.10	9.45	2.55	13	Karaganda, Kazakhstan	Kushev (1963)
Carnian	4.50	1.73	10.21	2.40	21	Ipswich, Australia	Mengel and Carr (1976)
Ladinian	0.41	0.08	1.93	0.51	13	Nymboida, Australia	McElroy (1963)
Tatarian	3.53	0.91	7.62	2.11	15	Newcastle, Australia	Pittman (1913)
Artinskian-Kungurian	6.01	1.90	21.20	5.06	14	Capella, Australia	Wilson (1975)
Sakmarian-Artinskian	3.21	0.70	9.54	2.92	20	Novokuznetsk, Siberia	Gorelova et al. (1973)
Westphalian	6.09	0.61	13.41	3.81	14	Sydney, Canada	Hacquebard and Donaldson (1969)
Visean-Namurian	2.68	0.50	5.80	2.03	20	Karaganda, Kazakhstan	Kushev (1963)
Tournaisian	3.78	0.45	7.85	3.11	5	Price Mountain, Virginia, U.S.A.	Campbell (1925)
Fammenian	0.23	0.15	0.37	0.12	3	Elkins, West Virginia, U.S.A.	Scheckler (1986)
Frasnian	0.07	0.03	0.25	0.08	8	Melville Island, Arctic Canada	Chi and Hills (1976)
Emsian-Elfeian	0.42	0.05	1.35	0.63	4	Barzas, Siberia	Ergolskaya (1936)

Many of these same sequences include the thickest individual coal seams for their time, but some exceptionally thick coals are in sequences of <10 consecutive seams (Table 2). Both sets of data reveal an increase in seam thickness from Early Devonian to Late Carboniferous, with the Late Carboniferous plateau sustained until the last coals of the Permian. As already discussed, no Early Triassic coals are known, and Middle Triassic coals are few and thin (Retallack, 1979; Retallack et al., 1977, 1993; Retallack and Ryburn, 1982). Our data showing thin coal seams of the Middle Triassic (Fig. 3) can be interpreted as a recovery phase from the coal gap. By Late Triassic and into the Jurassic, coal thickness reached values comparable with that of the Late Carboniferous-Late Permian. There is considerable variation in these data as a result of local paleoclimatic and tectonic settings of the coals, but the coal gap and its recovery remain prominent. The increased thickness of Devonian-Carboniferous coals can be attributed to evolutionary improvements in lignin or phenolic production, biomass, or productivity, which increased effectiveness of the peat-forming flora in persisting against disturbances such as storms, floods, decay, or herbivory (Diessel, 1992), or to a less-perturbed landscape (Shearer et al., 1994). Similarly, Middle Triassic peat swamps may have been re-evolving communities that could cope with disturbance or were in less-perturbed landscapes. By Late Triassic time, levels of disturbance resistance were attained that were comparable to

those abruptly curtailed at the Permian-Triassic boundary. The Middle Triassic recovery of coal thickness is similar to the Late Devonian-Early Carboniferous evolution of thick coal seams.

The petrographic composition of coals has changed through time, and this could reflect changes in the ability of swamp plants to resist physical disturbance and biological decay (Robinson, 1990). Carboniferous coals are rich in vitrinite, a maceral derived from cordaite and lycopod wood and bark (DiMichele and Phillips, 1994). Vitrinite-

rich coals remain common through every subsequent geological period, but Permian and younger coals have a greater proportion of macerals other than vitrinite (Diessel, 1992). Many Permian coals, for example, are very rich in inertinite macerals such as fusinite, which is thought to be charcoal from the burning of dry peat. Jurassic and younger coals are sometimes rich in exinite, such as resinite produced by conifers (Gould and Shibaoka, 1980). There has not yet been found a significant change in the petrographic composition of coal shortly before

TABLE 2. MAXIMUM THICKNESS OF INDIVIDUAL COAL SEAMS THROUGH TIME

Age	Thickness (m)	Locality	References
Holocene	13.7	Rajang Delta, Borneo	Anderson (1964)
Pliocene	9.5	Lajtanjalu, Hungary	Papp (1913)
Miocene	97.0	Yallourn, Victoria, Australia	Gloe (1984)
Oligocene	165.0	Morwell, Victoria, Australia	Gloe (1984)
Eocene	120.0	Gieseltal, Germany	Krumbiegel et al. (1983)
Paleocene	55.0	Powder River, Wyoming, U.S.A.	Ayers and Kaiser (1984)
Maastrichtian	36.6	Kaitangata, New Zealand	Harrington (1958)
Coniacian-Santonian	23.3	Kaiparowits, Utah, U.S.A.	Doelling and Graham (1972)
Aptian	17.0	Rasdolenski, Primorie, Russia	Krassilov (1992)
Barremian	48.0	Fuxin, Liaoning, China	Wu et al. (1992)
Callovia	15.5	Karaganda, Kazakhstan	Kushev (1963)
Bajocian	11.2	central Tadjikistan	Luchnikov (1982)
Toarcian	32.1	Karaganda, Kazakhstan	Kushev (1963)
Carnian	24.0	Callide, Queensland, Australia	Smyth (1980)
Ladinian	1.9	Nymboida, New South Wales, Australia	McElroy (1963)
Tatarian	29.0	Galilee Basin, Queensland, Australia	Smyth (1980)
Artinskian-Kungurian	21.2	Capella, Queensland, Australia	Wilson (1975)
Artinskian	37.0	East Bokaro, India	Casshyap and Tewari (1984)
Westphalian	30.0	Creusot, France	Defline (1913)
Visean-Namurian	11.2	Karaganda, Kazakhstan	Kushev (1963)
Tournaisian	6.2	Price Mountain, Virginia, U.S.A.	Campbell (1925)
Fammenian	0.4	Elkins, West Virginia, U.S.A.	Scheckler (1986)
Frasnian	0.3	Melville Island, Arctic Canada	Chi and Hills (1976)
Emsian-Elfeian	1.4	Barzas, Siberia	Ergolskaya (1936)

or after the Early Triassic that would implicate changing plant woodiness or decay resistance as a cause of the coal gap (Robinson, 1990).

EVIDENCE FROM PALEOSOLS

Many Early and Middle Triassic nonmarine sequences contain red beds (Fig. 1), which have been interpreted as indicating onset of desert to monsoonal climates at the beginning of the Triassic (Wang, 1993). The aridity and seasonality would have been very severe indeed if they eradicated peat formation globally, considering the peats now forming in climates as dry and seasonal as the "Sudd" of Sudan and Okavango Delta of Botswana (Lottes and Ziegler, 1994). In any case, evidence from the distribution of red beds and the detailed study of paleosols in red beds contradict the idea of globally dry Early Triassic paleoclimates.

Red beds are not restricted to the Early Triassic, but are widespread in the Carboniferous (Besly and Turner, 1983; Loope, 1988), Permian (Steel, 1974; Bull and Cas, 1989; Kent, 1980; Wang, 1993; Veevers and Tewari, 1995), Middle-Late Triassic (Hubert, 1977; Kraus and Middleton, 1987; Sereno et al., 1993), and Jurassic (Kitching, 1979; Dodson et al., 1980). The unique feature of Early Triassic nonmarine strata is not their red color, but their lack of coal.

Red color of beds is caused by local drainage and has little paleoclimatic significance in itself. Studies of paleosols in red beds indicate that the principal reason for their red color is oxidation in well-drained soils, as indicated by abundant burrows of non-aquatic animals, deeply penetrating root traces, abundant illuvial clay skins, and thorough chemical weathering (McPherson, 1980; Besly and Turner, 1983; Loope, 1988; Retallack, 1990, 1991). Enhanced reddening is due to dehydration of ferric hydroxides to oxides during burial, but the primary oxidation in most cases was during exposure to air in a soil (Retallack, 1991).

Red beds include paleosols representing a wide range of paleoclimates: wet and dry, monsoonal, and nonseasonal climates. Some Early Triassic red beds are sequences of paleosols with calcareous nodules of the kind expected (pedocals) in monsoonal semiarid climates—for example, paleosols of the Buntsandstein of Germany (Ortlam, 1971; Mader, 1990; Weber, 1993). Other Early Triassic sequences of red paleosols are noncalcareous, and in some cases deeply weathered to bauxitic (pedalfers), as is com-

mon in a humid nonseasonal climate, such as paleosols of the Bald Hill Claystone of Australia (Retallack, 1976, 1977a). These paleosols could be regarded as evidence of environmental acidification, but this was clearly not universal, considering calcareous Early Triassic paleosols found in other parts of the world.

In addition to red, formerly well-drained soils that formed in environments unsuitable for peat accumulation, there also are Early Triassic suites of paleosols that formed in waterlogged environments. Paleosols of the Early Triassic Newport, Garie, and Wombarra Formations of southeastern Australia include ganisters, siderite nodules, and sphaerosideritic fireclays similar to paleosols (including "underclays" and "fireclays") of Carboniferous coal measures of Europe and North America (Retallack, 1976). Kaolinitic and podzolized paleosols in these formations are also evidence for a humid paleoclimate (Retallack, 1977a). Yet the closest thing to a coal in the Newport Formation is thin carbonaceous claystone (Retallack, 1975). Thus humid wetland environments were present locally during the Early Triassic, but they did not accumulate peat. This line of evidence falsifies theories that the coal gap was due entirely to arid paleoclimate (Worsley et al., 1994) or low base level (Daragan-Sushchov, 1989; Faure et al., 1995).

EVIDENCE FROM PALEOZOOLOGY

The Permian-Triassic boundary has long been known as a major crisis for animal life in the sea, with extinction of >90% of marine species (Raup, 1979), including all fusuline foraminifera, trilobites, and tabulate and rugose corals. This profound break in the evolution of life has attracted a variety of environmental explanations, including impact of large extraterrestrial bolides, massive eruption of Siberian flood basalts, and unusually low sea level. Erwin (1994) has reviewed and proposed a combination of these—a "world went to hell" hypothesis.

Recent reassessment of the fossil record of insects (Labandeira and Sepkoski, 1993) and vertebrates (Benton, 1987) has demonstrated that the Permian-Triassic boundary was a time of crisis for animals on land as well (Fig. 1). Early Triassic vertebrate faunas are distinguished by both lower diversity and more cosmopolitan distribution than faunas of Late Permian or Late Triassic age (Parrish et al., 1986). The therapsid reptile *Lystrosaurus* dominates vertebrate assem-

blages of Early Triassic age in South Africa, India, Antarctica, China, and Russia (King, 1990). *Cynognathus* and *Rechnisaurus* are additional Early-early Middle Triassic (Scythian-Anisian) therapsid reptiles with wide geographic distribution (Parrish et al., 1986; de Fauw, 1993). During Late Triassic time vertebrate faunas were again diverse and provincial with the rise of rhynchosaurs and dinosaurs (Benton, 1987; Sereno et al., 1993). Both on land and in the sea, the coal gap was initiated during a period of biological extinction and followed by recovery from a protracted time of low biological productivity. Neither vertebrates nor insects anticipated or profited from the coal gap.

EVIDENCE FROM PALEOBOTANY

Plant extinction and evolution through the coal gap also can be examined from paleobotanical data. Although plant fossils can be abundant and diverse in coal measures, not all were necessarily peat formers. Fortunately there are rare permineralized peats in which peat-forming vegetation is preserved and can be compared with modern vegetation of mires (Table 3). Trunks of permineralized wood and fossil forests were not included in our compilation unless shown to be from a laterally continuous permineralized peat. Our compilation also includes only fertile organs such as sporangia and seeds, when these are present with vegetative remains named using form genera. These data can be used to reconstruct floristic diversity through time (Fig. 3).

Calcareous coal balls of Late Carboniferous (Namurian-Westphalian) age from the United States are mainly of tree lycopsids or cordaites (Phillips et al., 1974), with the latter common in marine-influenced peats (Raymond and Phillips, 1983). Following Middle-Late Carboniferous (Stephanian) extinctions, the dominant trees in swamps were marattialean tree ferns of the genus *Psaronius*. Permian permineralized peats from Queensland (Gould and Delevoryas, 1977) and Antarctica (E. L. Taylor and Taylor, 1990) are dominated by wood and leaves of the seed fern *Glossopteris*. Permian coal balls in Siberia are dominated by wood of endemic Rufforian and Voynovskyan cordaites, which are also abundant in associated shales (Meyen, 1982; personal observations of Retallack, 1984). Permian coal balls of China are dominated by cordaites and lepidodendrolean lycopsids (DiMichele et al., 1987), and permineralized peats of this age from France are dominated by

TABLE 3. FLORISTIC DIVERSITY OF PERMINERALIZED PEATS AND MODERN MIRES

Taxon	Age	Genera (no.)	Locality	References
Dicots	Extant	270	Worldwide	Goodall (1983)
	Miocene	2	Chert, Yakima Canyon, U.S.A.	Koppes (1994)
	Eocene	12	Princeton chert, Canada	Stockey (1987); Cevallos-Ferriz and Stockey (1988a, 1988b, 1989, 1990a, 1990b, 1991); Erwin and Stockey (1987); Stockey and Pigg (1991); Cevallos Ferriz et al. (1993)
	Paleocene	5	Deccan chert, India	Chitaley (1974); Nambudiri et al. (1987)
Herbaceous monocots	Extant	165	Worldwide	Goodall (1983)
	Eocene	1	Princeton chert, Canada	Erwin and Stockey (1989)
	Paleocene	4	Deccan chert, India	Chitaley (1974); Nambudiri and Tidwell (1978)
Palms	Extant	15	Worldwide	Goodall (1983)
	Eocene	1	Princeton chert, Canada	Erwin and Stockey (1984)
	Paleocene	3	Deccan chert, India	Chitaley (1974)
Gnetales	Extant	1	Worldwide	Goodall (1983)
	Carnian	1	Chinle coal balls, U.S.A.	Pigg et al. (1993)
Cycadophytes	Neocomian	2	Chert, Catamaran, Tasmania	Tidwell et al. (1987)
	Neocomian	2	Rajmahal chert, India	Sahni (1932, 1948); Bose et al. (1990)
	Ladinian	1	Fremouw chert, Antarctica	Taylor and Taylor (1990)
Conifers	Extant	17	Worldwide	Goodall (1983)
	Miocene	1	Chert, Yakima Canyon, U.S.A.	Koppes (1994)
	Eocene	2	Princeton chert, Canada	Basinger (1984); Stockey (1984)
	Eocene	1	Driftwood Creek chert, Canada	Stockey (1983)
	Cenomanian	1	Winton chert, Australia	Peters and Christophel (1978)
	Neocomian	3	Rajmahal chert, India	Bose et al. (1990)
	Carnian	2	Chinle coal balls, U.S.A.	Pigg et al. (1993)
Peltasperms and corystosperms	Neocomian	1	Chert, Catamaran, Tasmania	Tidwell et al. (1987)
	Ladinian	2	Fremouw chert, Antarctica	Pigg and Taylor (1990); Pigg, (1990)
Cordaite	Asselian	1	Autun chert, France	Galtier and Phillips (1985)
	Pennsylvanian	11	U.S. and European coal balls	Phillips (1980)
Glossopterids	Tatarian	2	Buckley chert, Antarctica	Pigg and Trivett (1994)
	Tatarian	1	Fort Cooper chert, Australia	Gould and Delevoryas (1977)
Lyginopterids and relatives	Asselian	2	Autun chert, France	Galtier and Phillips (1985)
	Pennsylvanian	20	U.S. and European coal balls	Phillips (1980)
Leptosporangiate ferns	Extant	18	Worldwide	Goodall (1983)
	Eocene	2	Clarno chert, U.S.A.	Arnold and Daugherty (1964)
	Neocomian	2	Chert, Catamaran, Tasmania	Tidwell et al. (1987)
	Norian	1	Chert, Sarawak, Indonesia	Gastony (1969)
	Ladinian	3	Fremouw chert, Antarctica	Millay and Taylor (1990)
Coenopterids and Marattiales	Tatarian	1	Buckley chert, Antarctica	Galtier and Taylor (1994)
	Tatarian	2	Fort Cooper chert, Australia	Gould and Delevoryas, (1977)
	Asselian	14	Autun chert, France	Galtier and Phillips (1985); Lesnikowska and Galtier (1992)
	Pennsylvanian	18	U.S. and European coal balls	Phillips (1980)
	Famnenian	1	Hampshire coal balls, U.S.A.	Gillespie et al. (1981)
Horsetails	Extant	1	Worldwide	Goodall (1983)
	Eocene	1	Clarno chert, U.S.A.	Brown (1975)
	Neocomian	1	Rajmahal chert, India	Bose et al. (1990)
	Ladinian	1	Fremouw chert, Antarctica	Taylor and Taylor (1990)
Calamites and sphenopylls	Asselian	7	Autun chert, France	Galtier and Phillips (1985)
	Pennsylvanian	9	U.S. and European coal balls	Phillips (1980)
Lycopods	Extant	2	Worldwide	Goodall (1983)
Tree lycopside	Asselian	1	Autun chert	Galtier and Phillips (1985)
	Pennsylvanian	2	U.S. and European coal balls	Phillips (1980)
Rhyniopsids	Pragian-Emsian	4	Rhynie chert, Scotland	Kidston and Lang (1921); Edwards and Edwards (1986)

horsetails (*Calamites*) and ferns (*Psaronius*; Galtier and Phillips, 1985).

When the fossil record of permineralized peat picks up again with thin, local coals in the Middle Triassic, it is with different peat-forming plants. In addition, these Middle

Triassic peat plants are provincial, as if different evolutionary lineages were reoccupying wetlands in different parts of the world. Some Middle Triassic permineralized peats from Antarctica are dominated by remains of the seed fern *Dicroidium* (Corystosper-

maceae, Peltaspermales), while others have mainly cycadophytes (*Antarcticycas*) and ferns (Farabee et al., 1989; E. L. Taylor and Taylor, 1990; T. N. Taylor et al., 1993). The most common plant in carbonaceous shale partings within Middle Triassic coals of New

Zealand and Chile is an enigmatic plant, *Linguifolium*, perhaps a seed fern or cycadophyte (Retallack, 1979; Retallack and Ryburn, 1982). Different plants again have been found in shales associated with thin Middle Triassic coals of Europe (Mader, 1990). Late Triassic–Early Cretaceous swamps were dominated by osmundalean tree ferns, dipteridaceous ferns, conifers, cycadeoids, gnetaleans, and pentoxylaleans, as indicated by permineralized peats from Arizona (Pigg et al., 1993), Sarawak (Gastony, 1969), Tasmania (Tidwell et al., 1987; White, 1991), and India (Sahni, 1932, 1948).

Permineralized peats include wetland fungi, which have also been invoked to explain the coal gap (Moore and Worsley, 1994). Both Permian and Triassic permineralized peats from Antarctica include a variety of endosymbiotic and saprophytic fungi (E. L. Taylor and Taylor, 1990; T. N. Taylor et al., 1993). The Triassic fungi in some cases show exceptional preservation, such as arbuscles of mycorrhizae, but all the fungi belong to groups with an older Paleozoic record (Stubblefield and Taylor, 1988). Plants of waterlogged environments were not protected from fungal decay, and there is no clear indication of change in fungal assemblages from Late Permian to Middle Triassic.

Paleobotanical data also is useful in refining the extent of the coal gap and associated Permian–Triassic life crisis (Vakhrameev et al., 1978; Anderson and Anderson, 1983; Mader, 1990; Retallack, 1975). Compression fossil floras and palynology offer greater temporal resolution than permineralized peats on changes in vegetation from Late Permian to Middle Triassic time. Although several assessments of fossil floras have stressed the gradual nature of floral change across the Permian–Triassic boundary (Knoll, 1984; Meyen, 1987), there are now indications of abrupt and widespread extinctions of plants at the boundary (Retallack, 1995). Abrupt extinctions of glossopterids, gigantopterids, voykovskyaleans, and rufioraleans at the Permian–Triassic boundary were unrelated to long-term diachronous change in dominance of gymnosperms over pteridophytes, which has been termed the *Paleophytic–Mesophytic transition* (Fredericksen, 1972; Gray, 1993). New radiometric dating (Vevers et al., 1994a) and international correlation of a marked carbon-isotopic shift in kerogen (Morante, 1993; Morante et al., 1994) indicate that the Permian–Triassic

boundary is immediately above the last glossopterid coal seam in the Bowen, Cooper, and Sydney Basins of Australia. New radiometric dating also places Siberian flood basalts at the Permian–Triassic boundary (Renne and Basu, 1991; Campbell et al., 1992; Renne et al., 1995). The distinctive fern-dominated Korvunchanian flora in the Siberian traps can be correlated with similar floras in coal-barren sediments overlying the last cordaites coals of the Kuznetsk Basin of Siberia (Gorelova et al., 1973; Betekhnina et al., 1984; Meyen, 1987).

In a continuous sequence of high temporal resolution across the Permian–Triassic boundary within the northeastern Sydney Basin (Herbert, 1993), palynological studies have shown abrupt extinction of the *Glossopteris* flora, with a dramatic transient increase of fern spores and acritarchs before establishment of a new and lower diversity flora (Grebe, 1970; Helby et al., 1987). A similar floral reorganization with a fern spike was found also in palynological studies of the Permian–Triassic boundary in Greenland (Hsü and McKenzie, 1990). This fern dominance may indicate ecological succession following catastrophic deforestation, as has been argued for the fern spike at the Cretaceous–Tertiary boundary (Nichols and Fleming, 1990). Also in the Sydney Basin, as well as in Europe and the Middle East, is a transient abundance of fungal spores and hyphae, which may reflect a brief episode of rotting of catastrophically destroyed vegetation (Visser and Brugman, 1988; Eshet, 1992; Retallack, 1995). Transient acritarch swarms at the Permian–Triassic boundary in Greenland, Pakistan, China, and southeastern and Western Australia are evidence for widespread marine incursions into predominantly nonmarine basins (Balme, 1989). These also indicate catastrophic changes at the boundary, and falsify the idea that the coal gap was the result of low sea level.

A catastrophic change in vegetation at the Permian–Triassic boundary is also apparent from the distinctive nature of Early Triassic plants, which are low in diversity and cosmopolitan compared with Late Permian plants (Meyen, 1987). Early Triassic vegetation is similar worldwide, with low-diversity assemblages dominated by voltziacean conifers (*Voltzia*, *Voltziopsis*) and herbaceous to weakly lignified lycopsids (*Annalepis*, *Cylomeia*, *Tomioostrobus*, *Pleuromeia*; Vakhrameev et al., 1978; Mader, 1990). These Early Triassic plants also show indications of adaptation to low nutrients or seasonal to sparse water supply in the form of

succulence, inrolled leaves, small leaves, needle leaves, and heterophylly (Mader, 1990). Gone were the latest Permian *Tatarina* flora of northern Pangea, the *Glossopteris* flora of the southern Pangea, and the *Gigantonoclea* flora of tropical China. It was not until Middle Triassic time that floral provincialism and diversity was reestablished with the *Scytodiphyllum* flora of northern Pangea and the *Dicroidium* flora of southern Pangea (Retallack, 1977b, 1980; Meyen, 1987). The oligotrophic depauperate interregnum of conifers and lycopsids, which appears abruptly at the Permian–Triassic boundary, corresponds in time with the worldwide spread of *Lystrosaurus* faunas, and with the coal gap.

Some paleobotanical support for the idea of a warm Early Triassic climate comes from Late Permian (E. L. Taylor et al., 1990) and Middle Triassic (E. L. Taylor and Taylor, 1993) permineralized forests in Antarctica, at paleolatitudes too cold for vascular plants today (Parrish et al., 1986). The presence of mosses in Permian (but not Triassic) peat, and of cycads in Triassic (but not Permian) peat may be an indication of a warmer climate in the Triassic (E. L. Taylor et al., 1989; E. L. Taylor and Taylor, 1993). On the other hand, depauperate conifer–lycopsid floras of the Early Triassic are like floras of cool climates today (Retallack, 1980), and the small fossil cycads of the Triassic did not have the large terminal meristem of frost-intolerant modern cycads (Spicer and Chapman, 1990). Furthermore, Early Triassic vegetation can be regarded as a product of a life crisis at the Permian–Triassic boundary (Retallack, 1995), in which case modern comparisons are weak. Permian–Triassic extinctions are a more attractive explanation for the coal gap considering the taxonomic differences between Late Permian and Middle Triassic peat floras, together with catastrophic extinctions of plants at the Permian–Triassic boundary associated with transient abundances of fungi, acritarchs, and ferns.

If the coal gap was initiated in a sudden catastrophe, there remains the problem of its 10 m.y. duration. One explanation could be that Permian–Triassic extinctions cut deeply into ecosystem components such as microbial nutrient procurement systems. This was the most profound life crisis in the history of life (Erwin, 1994), with severe microbial disruption indicated by transient abundances of acritarchs and fungi (Visser and Brugman, 1988; Balme, 1989; Eshet, 1992). A microbial crisis is indicated

also by the local abundance of cyanobacterial stromatolites in nonmarine (Mader, 1990) as well as marine strata of Early Triassic age (Schubert and Bottjer, 1992). The Permian-Triassic boundary crisis may have been severe enough to reset life on earth back to earlier simpler ecosystems without the mycorrhizae, nitrogen fixers, and other organisms required for the maintenance of vascular plants.

An additional biological explanation for the 10 m.y. delay of the coal gap is that adaptations to the acidic, oxygen-poor, and nutrient-starved conditions of swamps are rare. A striking feature of fossil plants in permineralized peats is their low diversity and relictual character, compared with coexisting plants of associated sedimentary rocks (DiMichele et al., 1987). Carboniferous peat-forming plants of North America belong to long-ranging, slowly evolving clades that were replaced only after long intervals at mass extinctions (Phillips et al., 1974). This may be an evolutionary consequence of the ecological observation that peat environments are difficult for plant nutrition and low in plant competition (DiMichele et al., 1987). In such difficult environments, the coevolution of plants and microbes may have taken longer than elsewhere on land.

COMPARISON WITH THE REEF GAP

The absence of fossil coral reefs, corals, and bryozoans in Early Triassic rocks has long been a puzzle (Erwin, 1994). The enigma is emphasized by impressive fossil reefs of sponges and brachiopods of Late Permian age in West Texas and of sponges and bivalves of Middle and Late Triassic age in the southern calcareous Alps of Europe. Middle Triassic reefs have similar overall facies and structure to Late Permian reefs, but many new organisms. These included scleractinian corals and cheilostome bryozoans very different from Paleozoic clades of corals and bryozoans, as well as persistent coralline algae and sclerosponges (Stanley, 1992; Flügel, 1994).

Tropical reefs and peat swamps are very different kinds of environments, but they do have common features. One of these is a narrow tolerance for changes in base level. Few reef organisms can withstand exposure to air for longer than an intertidal cycle. Corals with symbiotic zooxanthellae and red algae that are primary reef framework builders are restricted to the photic zone (Stanley, 1992). Similarly, peat will not accumu-

late in swamps if allowed to dry or become aerated enough for decay by microbial decomposers. On the other hand, subsidence beyond the rate at which trees can maintain some degree of aeration of their roots kills swamp trees and creates a lake rather than a swamp (Falini, 1965). Although this line of argument could implicate changes of sea level in their demise, reefs should still have been able to survive on evenly sloping volcanic islands and peats in intermontane basins.

A second common feature of reefs and peat swamps is oligotrophy, or nutrient starvation. Reefs grow best in clear waters distant from mouths of large rivers that deliver sediment and nutrients such as phosphorus (Hallock, 1987; Wood, 1993). Similarly, the waters of peat swamps are commonly too acidic for phosphorus and other cationic nutrients to be available to plants (Moore and Bellamy, 1974). By this reasoning, coral reefs and peat swamps should have survived better than other ecosystems during Permian-Triassic productivity collapse, but this was not the case. Coincidence in time of both the beginning and end of the reef and coal gaps implies a cause that affected both land and sea, such as the Permian-Triassic life crisis (Retallack, 1995).

A SUMMARY OF CAUSES OF THE COAL GAP

The various lines of evidence reviewed above are here summarized for possible explanations for the Early Triassic coal gap.

High Continental Freeboard

Although continents were riding high during the Late Permian and Early Triassic, this would not have destroyed wetlands in intermontane basins or oceanic islands. Global sea level curves and locally abundant marine acritarchs in nonmarine sequences of Early Triassic age indicate marine transgression shortly after the Permian-Triassic boundary, at the start of the coal gap. In addition, paleosols in some places, such as the Early Triassic Newport Formation of Australia, indicate humid bottomlands that at other times would have encouraged peat accumulation.

Environmental Acidification

Acid rain at the Cretaceous-Tertiary boundary produced a transient $^{87}\text{Sr}/^{86}\text{Sr}$ spike in marine carbonate, as unusual

amounts of old continental strontium were released to the ocean by weathering. A much broader perturbation of the strontium isotopic balance in the oceans extends from the Late (but not latest) Permian into the Early (but not earliest) Triassic, perhaps related to increased hydrothermal activity at mid-ocean ridges. Strong perturbations at the Permian-Triassic boundary in $\delta^{13}\text{C}$ of marine carbonate and kerogen and of nonmarine kerogen reflect a redox and productivity crisis, which could plausibly have involved also acid rain. These are short-term effects compared with the 10 m.y. duration of the coal gap. In addition there is evidence from calcareous paleosols of Early Triassic age in Germany, South Africa, and elsewhere that protracted acidification was not universal on land.

Paleoclimatic Change

Permineralized peats of Late Permian and Middle Triassic age in Antarctica are surprisingly rich in trees for such high paleolatitudes, and the poles may have been free of large ice caps at this time, but both Permian and Triassic peats contain fossil plant assemblages of temperate woodlands. The oxidation of carbon indicated by marked isotopic shift at the Permian-Triassic boundary and later rise of cycadophytes could signal the advent of a carbon dioxide greenhouse. Although a simple picture is often presented of a dry Triassic with red beds following a wet Permian with coal measures, recent interpretation of paleosols and evaporites presents a different and more detailed picture. Calcareous red paleosols indicate semiarid to subhumid climates during both the Permian and Early Triassic in the United States, Britain, and Europe. Noncalcareous kaolinitic paleosols indicate humid climates during both Permian and Early Triassic in Siberia, Antarctica, and Australia. There were extensive regions climatically suitable for peat formation during the Early Triassic.

Rise of Decomposers and Herbivores

The meager fossil record of fungi in Late Permian and Middle Triassic peats from Antarctica shows no obvious differences in fungal decomposers over this interval. Evolution of wetland fungi has also been implicated in the lack of tropical peat accumulation after the Carboniferous, but the shift of peat accumulation to high latitudes was already completed by Late Permian and was

maintained when coals reappeared during the Middle Triassic.

Plant-eating insects and reptiles had evolved to considerable diversity by Late Permian time, but were decimated by extinctions at the Permian-Triassic boundary. Early Triassic faunas were cosmopolitan and low in diversity, unlike either Late Permian or Middle Triassic faunas. Thus neither decomposers nor herbivores anticipated or profited from the demise of peat swamps at the Permian-Triassic boundary.

Extinction of Coal Flora

The Permian-Triassic boundary was a time of crisis for plants, when globally diverse and highly provincial vegetation largely of seed ferns was replaced abruptly by a low-diversity cosmopolitan vegetation of conifers and lycopsids. Low Early Triassic productivity also is indicated by depleted $\delta^{13}\text{C}$ values of carbonate and kerogen on both land and sea. Extensive peat swamps in Siberia, China, Australia, South Africa, and Antarctica disappeared along with their distinctive voykovskyalean and rufiorialean cordaites and glossopterid seed ferns at the Permian-Triassic boundary. Plants are slow to adapt to the difficult acidic and nutrient-poor substrates of peat swamps. The Permian-Triassic life crisis reached deeply into microbial levels of terrestrial ecosystems, as indicated by widespread transient abundances of fossil acritarchs, fungi, and stromatolites at the Permian-Triassic boundary.

Of the various explanations considered, we prefer to explain the Early Triassic coal gap as a consequence of extinction without replacement of peat-producing plants at the Permian-Triassic boundary. The recovery phase can be regarded as the re-evolution of tolerance to these acidic dysaerobic substrates by new groups of peat-producing plants during the Middle Triassic. Similarly the Early Triassic reef gap may be a consequence of extinction at the Permian-Triassic boundary of many kinds of reef corals and sponges. Explanations of the Permian-Triassic extinctions themselves are beyond the scope of this study, but in ongoing debates about this singular event, the Early Triassic coal gap now can be considered another part of its legacy.

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